

ON THE RELATIONSHIP OF *STREPTANTHUS VERNALIS* AND
STREPTANTHUS BARBIGER (BRASSICACEAE)

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ABSTRACT

The relationship between *Streptanthus vernalis* and *Streptanthus barbiger* (including the taxonomic synonym *Mesoreanthus fallax*) is examined. Morphological and allozyme comparisons show that the species are unrelated.

Key Words: E. L. Greene, *Mesoreanthus*, *Streptanthus vernalis*, allozyme analysis.

Streptanthus vernalis O'Donnell and Dolan is a newly described species from Three Peaks in Lake County, CA (O'Donnell and Dolan 2005). In the paper describing this species, O'Donnell and Dolan (2005) compared *S. vernalis* morphology to that of sympatric *Streptanthus* species and to *S. batrachopus* J. Morrison, a species known only from Marin County, CA (*S. batrachopus* was included because some observers of *S. vernalis* thought that it was *S. batrachopus*). We also performed allozyme analysis to measure the genetic distance between *S. vernalis* and other *Streptanthus* species.

The possibility that *S. vernalis* is *Mesoreanthus fallax* E. Greene has been raised (Dr. Dean Taylor personal communication 2006). *Mesoreanthus fallax* is a taxon segregated from *S. barbiger* E. Greene by Greene because of perceived morphological differences, examined below. *Streptanthus barbiger* was not included in the comparisons in O'Donnell and Dolan (2005) because we did not consider it to be related to *S. vernalis*, and there was no population of *S. barbiger* within 15 kilometers of the only known *S. vernalis* population. However, to address the possibility that *S. vernalis* is *M. fallax*, in this paper I compare *S. vernalis* to *S. barbiger*.

STREPTANTHUS BARBIGER

Streptanthus barbiger, a widely distributed but uncommon serpentine endemic of the inner Coast Range of northern California, was first described by Greene (Greene 1888) based on a specimen collected in June 1888 by A. B. Simonds from Highland Springs, Lake County, CA. The specific epithet *barbiger* (bearded) presumably referred to the "short bristly white pubescence" which was perceived on the tips of the sepals. Greene supplemented his description of *S. barbiger* (Greene 1894), adding that the entire calyx, not just the sepal tips, was "commonly bristly-hairy, but often glabrous". He noted elsewhere that it was common in Napa Co.,

specifically at Miravalle, an estate west of the town of St. Helena.

Later, Greene split *S. barbiger* into three species under the generic name *Mesoreanthus* (Greene 1904, 1903–1906): (1) *M. barbiger*, the "type species", with hirsute sepals; (2) *M. fallax*, a glabrous, glaucous species collected in July 1891 in the hills above St. Helena in the Napa Valley; and, (3) *M. vimineus*, also glabrous and glaucous, which Greene described as a showier plant with large white blossoms. *Mesoreanthus vimineus* was collected by C.F. Baker in early May 1903 near Lakeport.

The specimens of *M. fallax* that Greene used to describe that new species were fruiting and had few blossoms and no leaves; thus, his description is sketchy and incomplete. Perhaps it was their lack of leaves that prompted Greene to apply the specific epithet *fallax* to the poor specimens he found: *fallax* means "unclear, deceptive". A topotype of *M. fallax* in the California Academy of Sciences herbarium (Greene 16323, CAS 296902) appears to be typical *S. barbiger*: the basal leaves are oblanceolate, entire, with a purple cast, and the cauline leaves are linear. The calyx is almost glabrous. However, all four of the white petals are marked with purple where usually only the two lower are so marked. Only one other *M. fallax* accession known to the author is Greene's of 1891 in the Harvard Herbarium (Barcode 40579); one specimen in the University of California Herbarium of *S. barbiger* (UC10858) has been annotated *M. fallax*, annotator unknown.

Streptanthus barbiger is described by Buck et al. (1993) in The Jepson Manual as a variable species, a characterization confirmed by the significant variation in descriptions of *S. barbiger* since it was first described, as indicated on Table 1. Buck et al. (1993) may have found additional justification for their description because they lumped unidentified plants from Tehama and Lake Counties under *S. barbiger*. A coauthor of Buck et al. (1993) says he "lumped several things under *Streptanthus barbiger* E.

TABLE 1. COMPARISON OF THE MORPHOLOGICAL CHARACTERS OF *STREPTANTHUS VERNALIS* AND *STREPTANTHUS BARBIGER*.

| | <i>Streptanthus vernalis</i> O'Donnell & Dolan (2005) | <i>Streptanthus barbiger</i> Greene (1888) | <i>Mesorecanthus fallax</i> Greene 1904 | <i>Streptanthus barbiger</i> Jepson 1936 | <i>Streptanthus barbiger</i> Munz (1959) | <i>Streptanthus barbiger</i> Buck et al. (1993) |
|------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Flowering period | annual, March–May 2–20 cm | annual 12 in. (30.5 cm) erect, slender | annual, ?–July 1–2 ft (~3–6 dm) slender, glabrous, glaucous, freely branching from base | annual, June–July 1–2.25 ft (~3–7 dm) stem with erect branches from above the base | annual, May–July 3–7 dm glabrous, glaucous, erect, branched above | annual 1–8 dm generally branched throughout |
| Habit | usually simple or branched from below | erect, slender | slender, glabrous, glaucous, freely branching from base | stem with erect branches from above the base | glabrous, glaucous, erect, branched above | generally branched throughout |
| Inflorescence | racemose, sometimes second | loosely racemose- paniculate, glabrous throughout except calyx | fruiting spikes long and lax | racemes mostly a little loose, second, often markedly so | lax raceme 5–25 cm long; pedicels erect 2–3 mm long | |
| Leaf | basal: orbicular, apically crenate, green above, purple below, succulent, 3–4 cm, petiole 1 mm, apical teeth orange- tipped; cauline: narrowly lanceolate but never linear; entire, sessile, orange-tipped | linear, entire | unknown | 1–6 in. (2.5–15.25 cm) long; the blades linear to elongated linear- lanceolate, entire, or the lower dentate, auriculate at base, or not at all auriculate; sessile, or drawn down to a short petiole | sublinear, erect, entire; lower 6–10 cm long; upper very narrow, reduced | basal +/- not rosetted, lower blades <7 cm, oblanceolate to widely obovate, generally coarsely dentate, petioled; middle and upper cauline leaves <11 cm, +/- linear, generally +/- entire, generally sessile, sometimes +/- clasping |
| Calyx | biradial, glabrous | subsessile, 4 lines long | subsessile, small | — | — | — |
| Sepal | 6–7 mm, green, yellow toward tips | nearly equal and alike, greenish white with white tips clothed with a short bristly white pubescence | tips very long, spreading and recurved, equally or exceeding petals | greenish with whitish or membranous recurved tips | green to purplish, hyaline on margins and recurved tips, sometimes with stiff hairs but no apical tuft, 6–7 mm long | 3–6 mm, generally greenish yellow (purplish), generally +/- glabrous |
| Petals | white, strongly reflexed, 2 mm | white | small, dark-red, white edged | 3 lines long; limb rounded; not crisped or scarcely; upper pair white; lower pair white with purple band from claw running nearly from center of limb | about 1 cm long, not crisped, upper pair white; lower pair with purple midvein | 5–10 mm; upper +/- whitish; lower generally purple (rarely whitish) |

TABLE 1. CONTINUED.

| | <i>Streptanthus vernalis</i> O'Donnell & Dolan (2005) | <i>Streptanthus barbiger</i> Greene (1888) | <i>Mesoreanthus fallax</i> Greene 1904 | <i>Streptanthus barbiger</i> Jepson 1936 | <i>Streptanthus barbiger</i> Munz (1959) | <i>Streptanthus barbiger</i> Buck et al. (1993) |
|---------|---------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------|----------------------------------------------------------------------|----------------------------------------------------------|----------------------------------------------------------|
| Stamens | three pairs; uppermost broadly connate, exerted, recurved; middle, inserted fused to middle; lowest: free, inserted | in three very unequal pairs; filaments: dark purple, the uppermost pair united almost to the summit; anthers: linear-sagittate, white narrowly linear, recurved | upper pair equal to sepals; filaments: upper pair united to summit; anthers: upper pair very small | filaments: upper united at top; lower united halfway | filaments: upper connate | filaments: upper pair fused; anthers: upper pair reduced |
| Silique | erect, up to 4-5 cm, torulose | very narrow, compressed, slightly torulose, 1.5 in. (3.8 cm) long, curved downwards on very short spreading pedicels oval, little compressed, marginless | reflexed or reflexed spreading; slightly curved; obscurely torulose | spreading, somewhat recurved, sessile 5-7 cm long, about 1.5 mm wide | spreading, 2-7 cm +/- curved, +/- narrowed between seeds | |
| Seed | orange, winged | — | not winged | not winged | wing: 0 or at one end | |

Greene" in his treatment of the species (Dr. Dean Taylor personal communication). Thus, *S. barbiger* as described in Buck et al. (1993) is probably not a single entity but rather a collection of entities.

Table 1 compares *S. vernalis* to *S. barbiger* (including the synonymous *M. fallax*) as it was described by Greene and subsequent authors. Table 1 retains the language from the descriptions of *S. barbiger* to preserve the intentions of each author as to diagnostic characters. This results in some cases in different measurements of the organs (e.g., centimeters, inches, lines) and different characters being featured. Notwithstanding the diversity of descriptive choices that the authors from Greene to Buck et al. (1993) have made, the morphological differences between *S. vernalis* and *S. barbiger* are clear.

COMPARISON OF MORPHOLOGY

The treatments of *S. barbiger* shown in Table 1 indicate a wide range of variation in important characters: height, calyx vestiture, and the purple veining on the lower petals. The siliques are variously described as recurved/reflexed and spreading, and spreading only; the torulose character of the silique has remained faint. The branching pattern varies widely, from branching from the base, to branching above, to generally branching; there appears to be no consensus on the branching. As for the leaves, the authors focus on the narrow, linear cauline leaves. Jepson (1936) and Buck et al. (1993) mention the lower cauline leaves which are long, wide and crenate (or coarsely dentate); none of the authors indicate that these leaves are often blotched with grayish irregular marks.

Specimens observed by the author near the Highland Springs Road in 2006 possessed bristly calyces, white upper petals, the lower pair marked with purple veining, and recurved siliques. Some of the individuals possessed long, crenate basal leaves, and all possessed linear, almost filiform cauline leaves.

In May 2007, a drought year, the author found an early flowering population of *S. barbiger* near the Highland Springs Reservoir. This population was generally shorter than other populations observed in nearby locations in previous years (<13 cm) and its other organs proportionately smaller than those found a few miles up the Highland Springs Road in 2006. The basal leaves were erect, clustered at the base and were entire or coarsely dentate; the cauline leaves were linear, filiform. The flowers, however, were typical of *S. barbiger*; i.e., upper petals white, lower petals white with purple veining. The author also observed a population of *S. barbiger* on Spring Mt. Road west of St. Helena in July 2007. The plants of this population had glabrous calyces,

recurved siliques and, except for the basal leaves, which were no longer present, were otherwise identical to those found along the Highland Springs Road in 2006. The author cannot confirm that this Spring Mt. Road population was that from which Greene sampled, or the source of the specimen in the California Academy of Sciences herbarium. Serpentine habitat in the area, including the former Miravalle estate, west of St. Helena is limited to a narrow band surrounded by volcanic substrate. Since Greene's time, the area has been planted with vineyards. It is possible that vineyards or other construction have replaced the *S. barbiger* populations that Greene observed.

The comparisons in Table 1 show that *S. vernalis* does not resemble *S. barbiger*. *S. vernalis* has no purple color in its petals or sepals, and the silique is erect and distinctly torulose. The seeds are winged. The leaf morphology of specimens of *S. barbiger* from Napa, Lake and Sonoma Counties in the Jepson Herbarium and at the California Academy of Sciences herbarium is very distinct from that of *S. vernalis*. The basal leaves of the former are usually oblanceolate and deeply crenate (sometimes entire) and the cauline leaves are entire, linear and sometimes filiform. This is true for the cauline leaves of specimens observed by the author in the hills west of St. Helena (Spring Mountain Road), the type locality of *M. fallax*, and for the specimens from Highland Springs, the type locality of *S. barbiger*. The leaf characters of these specimens are entirely different from those of *S. vernalis*.

Streptanthus vernalis does not resemble the toptotype of *M. fallax* in the herbarium of the California Academy of Sciences or *M. fallax* as Greene described it. *S. vernalis* does not have the very long spreading sepals reported for *M. fallax*. Where *M. fallax* is described as having dark-red lower petals edged with white, the lower petals of *S. vernalis* are white, suffused with a yellow tint and the upper petals are pure white (pers. obs.). Greene describes the fruiting racemes of *M. fallax* as "long and lax"; the fruiting branches of *S. vernalis* are short and retain their ascending and erect stature (pers. obs.)

TAXONOMIC STATUS OF *MESOREANTHUS FALLAX*

After Greene segregated the glabrous species *M. fallax* from the "type species" *M. barbiger*, *M. fallax* was not used. In the *Flora of Middle Central California* (Jepson 1911) Jepson lists *S. barbiger* but does not refer to *M. fallax*. Much later in Vol. 2 of the *Flora of California* (Jepson 1936), Jepson refers to both *M. fallax* and *M. vimineus* as synonyms of *S. barbiger* as does Abrams (1944). It appears that the glabrous calyx that had distinguished *M. fallax* from *M. barbiger* was assimilated into *S. barbiger*. Only

TABLE 2. NEI'S UNBIASED GENETIC IDENTITY (NEI 1978) VALUES FOR PAIRWISE COMPARISONS OF *STREPTANTHUS VERNALIS*, *S. BREWERI* SSP. *BREWERI*, AND COLLECTIONS FROM THREE DIFFERENT LOCATIONS FOR *S. BARBIGER*.

| | <i>S. vernalis</i> | <i>S. breweri</i> | <i>S. barbiger 1</i> | <i>S. barbiger 2</i> |
|----------------------|--------------------|-------------------|----------------------|----------------------|
| <i>S. vernalis</i> | * | * | * | * |
| <i>S. breweri</i> | 0.600 | * | * | * |
| <i>S. barbiger 1</i> | 0.298 | 0.526 | * | * |
| <i>S. barbiger 2</i> | 0.365 | 0.593 | 0.992 | * |
| <i>S. barbiger 3</i> | 0.204 | 0.408 | 0.891 | 0.842 |

Munz and Keck (1959) and Abrams (1944) mention the occasional hairy calyx in *S. barbiger*. Jepson (1936) remarked:

Greene (Fr. Fl.) describes the calyx as "bristly-hairy", an apparently unusual character for *S. barbiger* as we now know it. The calyces sometimes exhibit parallel hairlike lines in relief which imitate appressed bristles. However, the entire breweri-barbiger-niger series is unusually productive of variables, even for *Streptanthi*

No *Streptanthus* species with the characters of *M. fallax* appears to have taken its place. The only specimens in herbaria attributed to *M. fallax* in the Missouri Botanical Garden's TROPICOS database is Greene's of 1904/05. It appears that systematists since Greene have not recognized *M. fallax* as a separate species. While the name may be conserved, it cannot be applied to *S. vernalis*; morphological and allozyme evidence (see below) against such application is unambiguous: *S. vernalis* is not *M. fallax*. In fact a *M. fallax* was recently (Al-Shebaz and Taylor 2008) relegated to the synonymy of a new species *S. vinineus* Al-Shebaz & D. W. Taylor, and as no claim is made that *S. vinineus* is the same as *S. vernalis* the question is moot. To complete the reassignment of the genus *Mesoreanthus* I use this opportunity to consign the name *M. barbiger* to the synonymy of *S. barbiger*.

MOLECULAR ANALYSIS

Allozyme analysis was conducted by Dr. Rebecca Dolan (written comm. July 2007) on samples from three *S. barbiger* populations (Barbiger 1—Highland Springs Reservoir; Barbiger 2—Highland Springs Road about 2 mi west of Highland Springs Reservoir; and Barbiger 3—Spring Mt. Road), one *S. breweri* ssp. *breweri* population, and the sole population of *S. vernalis* following the procedures of Dolan (1995). Pairwise values of Nei's genetic identity (Nei 1978) in this analysis show *S. vernalis* to be most similar to *S. breweri* and very distant from the samples of *S. barbiger*. The three *S. barbiger* samples are very similar, with an average identity value of 0.91.

However, the *S. barbiger* populations in the vicinity of Highland Springs are more closely allied to each other than either is to the Spring Mountain Road population.

The data in Table 2 supplement the data in the original paper (O'Donnell and Dolan 2005). Notwithstanding the similarity to *S. breweri* ssp. *breweri* shown in Table 2, *S. vernalis* remains most closely allied to *S. morrisonii*, a sympatric species, as shown in the original paper.

CONCLUSION

Streptanthus barbiger and *Streptanthus vernalis* are separate species. Morphology alone is sufficient to distinguish the two species. Molecular analysis supports the distinction, and points to different origins for the two species.

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